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lies in endowments either in connection with universities, or through the establishment of the specialized private institution.

That the problem of applied evolution will eventually be solved there can be no doubt. That it will occur in our generation may only be expressed as a hope.

L. B. WALTON

KENYON COLLEGE,  
November 15, 1913

#### THE MUTATION MYTH

It has long been recognized both on the botanical zoological sides, that sterility is a notable characteristic of species crosses or true hybrids. Where species are nearer to one another their resultant cross is naturally less sterile than when their affinity is more remote. In the case of plants it is usually particularly easy to trace even slight evidences of previous hybridization in the sterility and abortive character of some of the spores or pollen. In contrast to hybrids, genetically pure species are characterized by pollen grains or spores, as the case may be, which are all perfectly developed. I have satisfied myself by a very extensive study of the spores and pollen of liverworts, mosses, ferns (including numerous genera of all the important families, isosporous and heterosporous), lycopods, selaginellas, quillworts, lepidodendroids, equisetas, cycads, ginkgo, conifers (including numerous genera of all the tribes), gnetales (all the genera) and many dicotyledonous and monocotyledonous angiosperms, that in good species the spores or pollen is invariably perfect morphologically, that is fully formed and having normal protoplasmic contents. Known hybrids on the contrary are characterized by a greater or smaller number of abortive spores, which have little or no protoplasmic contents. Hayes, of Connecticut, Pearl, of Maine, Emerson, of Nebraska, Dean Davenport, Rietz and Smith, of Illinois, are familiar to all interested in the application of the principles of evolution. One often conjectures, however, as to the extent to which some of the most valuable contributions are in reality "by-products" of investigations meeting the approval of the "Missouri" type of legislator.

This conclusion is by no means new but the wide range of facts examined in the present connection adds very materially to its strength. It has been further noted that so far as morphological conditions are concerned, plants of genetic purity, even when grown under extremely abnormal conditions, as exotics in greenhouses, etc., have perfect spores or pollen. For example a conifer or a cycad from Australia or Japan, grown in the hothouse and producing its pollen in the winter season, still shows the grains normally developed morphologically, whatever may be their physiological inefficiency.

The bearing of the facts indicated in the paragraph above is of great importance in relation to the mutation hypothesis of De Vries. This distinguished Dutch plant physiologist, a little over a decade ago, published a series of observations and generalizations under the title of "Die Mutationstheorie." His notable offering was the statement that material of a species of *Oenothera* or evening primrose, referred by him to Serigne's *Oenothera lamarckiana*, found growing spontaneously near Hilversum in Holland, was producing annually new species or as he preferred to call them, elementary species. In 1904 Professor De Vries was invited to lecture in the University of California on his sensational discoveries. The lectures were edited and published later by the director of the Desert Laboratory of the Carnegie Institution of Washington, with the title of "Species and Varieties, Their Origin by Mutation." Dr. MacDougal thus became both in fact and figuratively, the "*vox in deserto clamantis*," the baptist of the gospel of mutation. His exploits with the syringe in the baptism and production of new species of plants by intraovarial injections appear further to render his claims in this direction beyond question. As secretary of the Botanical Society of America and by his repetition and elaboration of De Vries's cultures of *Oenothera*, he has done unquestionably more than any one else to diffuse the doctrine of mutation in North America. It has in fact become so widely accepted on our continent, that it has in many instances

been unfortunately introduced even into elementary courses of botanical or biological instruction. Europe has presented a marked contrast to America in this respect, for here the mutation hypothesis of De Vries has been coldly received. It seems clear however that the European attitude is more in accordance with the established principles of biology than our own.

The distinguished English geneticist Bateson was apparently among the first to point out that in all probability *Oenothera lamarckiana* was a hybrid, as shown by the partial sterility of its pollen. Dr. MacDougal countered by the statement that he had found abortive pollen in specimens of *O. biennis*, growing in the vicinity of the city of New York. This he apparently regarded as a sufficient reply to Professor Bateson's criticisms. More recently a number of American students of plant genetics have cast doubt on the genetical purity of De Vries's *Oenothera lamarckiana*. Among these may be mentioned Davis, East, Emerson and Gates. The attitude of the last investigator is not the less significant because he was in the first instance a convinced mutationist of the De Vriesian school. In the case of the mutation hypothesis, we find again what is apparently an all too common condition in the case of biological theories, a neglect of fundamentally important morphological evidence. There seems to be absolutely no doubt, on morphological grounds, that not only is *Oenothera lamarckiana* of hybrid origin; but that the Onagraceæ, to which it belongs, are somewhat generally contaminated by spontaneous hybridism.

I have delayed publication of my conclusions in regard to the genetical status of the Onagraceæ, in the hope that some other morphologist would lay bare the extremely insecure foundations upon which the imposing superstructure of the mutation hypothesis has been raised. About eight years ago cultures of *O. lamarckiana* and its mutants were started at the Harvard Botanic Garden from seeds supplied by Professor De Vries. *Oenothera grandiflora*, which was of special interest in connection with the mutation hypothesis, was

likewise grown from seed supplied by Professor S. M. Tracey who made a special visit to Tensaw to obtain it for me. Shortly afterwards other work became more pressing and monopolized all available time. The cultures and seeds were accordingly turned over to Professor Bradley M. Davis, who was residing in Cambridge at that time. Dr. Davis has published a number of papers on hybridization work with *Oenothera* species and I have supplemented my original stock of preserved material from specimens kindly supplied by him.

Some illustration of pollen conditions in known hybrids other than Onagraceæ will first be considered. Many of our improved horticultural plants are known to have originated by hybridization, while others more anciently cultivated by our species are suspected of hybrid origin. Taking only the known hybrids as illustrations, such as tulips, irises, narcissus, lachenalia, freesia, etc., etc., we find that although many of the pollen grains are perfectly developed both as regards external form and internal contents, a greater or smaller proportion are small, shrivelled and nearly or quite devoid of protoplasm. In the case of genetically pure species of these genera the pollen grains on the contrary are all alike and perfect. In normal species, even when long in culture and under hothouse conditions the pollen has proved in all the cases examined in the present connection perfectly sound. This is notably the case for example with the common easter lily. The effect of hybridization is equally clear in the case of the Dicotyledons. Our pinks, calceolarias, nasturtiums, etc., are often of known hybrid origin and show clear evidence of such derivation in the condition of their pollen, which is more or less abortive. President Brainerd, of Middlebury College, has in recent years made some interesting observations on spontaneous hybrids of our native violets. He has found numerous forms of these, significantly described by certain systematists as new species, to be in reality hybrids, as shown by their characters clearly intermediate between recognized species and by their Mendelian segre-

gation in cultures. Professor Brainerd has been kind enough to supply some flowers of these interesting specimens for the present work and the pollen conditions are clearly those found in hybrids.

We may now profitably turn our attention to the Onagraceae, to which the well-advertised *Oenothera lamarckiana* belongs. Our common garden fuchsias are known to be of hybrid origin. In some of the varieties the pollen sterility is almost complete. This is notably the case in a hybrid derivative of *Fuchsia triphylla*, grown in the Harvard garden. In other varieties the sterility is often less marked. This condition has been found to obtain for example in long-tubed fuchsia hybrids. Here a certain number of the grains are perfectly developed and have normal protoplasmic contents, while others are small, shrivelled, collapsed and without protoplasmic contents. Among the wild-growing species of the Onagraceae, those of *Epilobium* have long been recognized by European systematists as prone to produce spontaneous hybrids. A good illustration in the present connection is supplied by a hybrid form of *E. hirsutum*, occurring commonly in the vicinity of ballast heaps. Here the pollen is to a large extent abortive, the degeneracy sometimes affecting the whole of the contents of the anther sack or in other cases being confined to a greater or smaller number of the grains. In contrast to *E. hirsutum* may be mentioned our common fireweed, *E. angustifolium* (sometimes put under a different genus). In all the abundant material of this species examined the pollen was entirely normal. Indications of hybridization correlated with corresponding pollen conditions have also been noted in the case of other representatives of the Onagraceæ, but the illustrations mentioned will suffice for our present purposes.

We may now turn to the genus *Oenothera* itself. In his "Mutationstheorie" De Vries has noted that about one third of the pollen of *O. lamarckiana* is sterile, and abortive. This statement I can only confirm. Even in the more vigorous of the so-called mutants originating in cultures of *O. lamarckiana* from

the seed, the pollen is very largely degenerate and in the less vigorous elementary species often almost completely so. In *O. lata* (mutant of *O. lamarckiana*) the pollen is frequently entirely sterile. But it is not only in *O. lamarckiana* and its so-called mutants or elementary species, that pollen sterility is to be seen, for this condition is well nigh universal in the species of this Onagraceous genus, recognized in systematic works. For example in the very common and variable species known as *O. biennis*, half of the pollen grains are sometimes abortive. This condition I have observed in specimens from regions as far apart geographically as the state of Massachusetts, the province of Ontario and the shores of the Gulf of St. Lawrence. The examination of a large amount of material of recognized wild species of *Oenothera* has led me to the apparently inevitable conclusion that spontaneous hybridism is extremely common in the genus and that in general it represents a condition of high genetical impurity. The purest species which has come under my notice, so far as may be judged from the pollen conditions is *O. grandiflora*, obtained from Tensaw. Here pollen abortion is well nigh absent both in flowers gathered for me by Professor Tracey and in those produced from seed both by Professor Davis and myself. Continued growth in the Harvard botanic garden has not altered this characteristic in any degree, for specimens grown last summer show the same condition of relative genetical purity or at least freedom from inharmonious hybridization.

It may be argued by some that the more or less marked constancy of the generally accepted species of *Oenothera* makes it clear that they are normal species. It is now recognized however that constant hybrids are of extremely common occurrence both in nature and as a result of experimental crossing. This is particularly true of species crosses. There is consequently no good reason why we should not admit that the genus *Oenothera* is strikingly characterized by spontaneous hybridization. There appears in fact to be every reason to believe that the bar sinister has been crossed and double crossed in our American

evening primroses. The extensive studies which I have made on the pollen and spore conditions in the higher plants from the mosses upwards, which will be detailed and illustrated elsewhere, make the conclusion apparently unavoidable, that the Onagraceæ in general and the genus *Oenothera* in particular, are peculiarly subject to spontaneous hybridization in nature. It follows of course that no genus or group of plants could have been more unfortunately chosen to illustrate the origin of species by mutation or saltatory evolution. Obviously we must in the light of the considerations advanced above, interpret the variability of the seedlings of *Oenothera* species, particularly of those of *O. lamarckiana* of De Vries, as evidence of ancestral hybridization, on the evidence of the very significant pollen conditions revealed both by the genus under discussion and by many members of the family to which it belongs.

The mutation theory of De Vries appears accordingly to lag useless on the biological stage and may apparently be now relegated to the limbo of discarded hypotheses. The zeal, industry and insight of the distinguished plant physiologist of Amsterdam can not be too highly appreciated. Even although his hypothesis must apparently be given up both on morphological and genetical grounds, it has nevertheless been the cause of a great deal of valuable work, which will remain after the motive of it has disappeared. The present refutation has been undertaken in the interest of biological progress in this country. It is now high time, so far as the so-called mutation hypothesis, based on the conduct of the evening primrose in cultures, is concerned, that the younger generation of biologists should take heed lest the primrose path of dalliance lead them imperceptibly into the primrose path to the everlasting bonfire.

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#### DEMOCRACY IN UNIVERSITY ADMINISTRATION<sup>1</sup>

A DISCUSSION of the topic assigned to me in this conference might be as brief as the fam-

ous chapter on snakes in the Natural History of Iceland, or, to use a more modern instance, as a review of Mr. Taft's activities in subversion of the courts and the constitution. There is no democracy in university administration. But we can consider the conditions and the remedies.

The situation of a teacher has aspects inherently undemocratic. He has arbitrary authority over the conduct and intellectual life of his students, and is paid by superior officials to discipline and teach as they prescribe. The professor may lecture to his classes "als dictirt euch der heilig' Geist," and in other academic relations may realize that silence is silver and flattery gold. To be half tyrant and half slave does not strike the average of a free man. The pedagogue may be expert in his narrow field, while he is segregated from the larger life of his fellow men. His salary is safe and small; his clothes are black and threadbare; he is very respectable, but only half respected. The inevitable difficulties we emphasize by providing on the one side a system of education which does not carry its own appeal and must be enforced by examinations, grades, degrees, compulsory attendance and the like, while on the other side a system of administration has developed which puts the professor in a position of personal dependence. He is not only unfree in the sense of the domestic servant, whose wages, work, company, habits and Saturdays off are set by the employer, but he is also unfree in the sense of the slave in that he is held to his place by forces that he can not resist. This may be in part caricature, like the typical professor of the novel or play who hunts beetles, while his daughter or wife engages in flirtation, but a caricature may depict and enforce the truth.

A less obvious but equally undemocratic aspect of the academic career is due to the fact that the university professor earns his living by teaching and the conduct of academic routine, while society depends on him

<sup>1</sup> Read at the conference on "The Relation of Higher Education to the Social Order," arranged by the council of the Religious Education Association, Yale University, March 5, 1914.